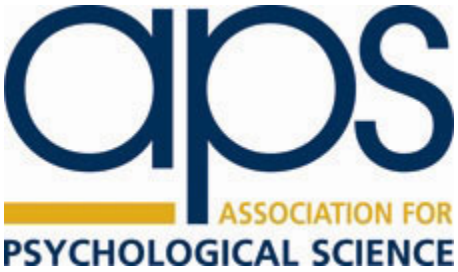

Research Report

Microsaccades Keep the Eyes' Balance During Fixation

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ABSTRACT—*During fixation of a stationary target, small involuntary eye movements exhibit an erratic trajectory—a random walk. Two types of these fixational eye movements are drift and microsaccades (small-amplitude saccades). We investigated fixational eye movements and binocular coordination using a statistical analysis that had previously been applied to human posture control. This random-walk analysis uncovered two different time scales in fixational eye movements and identified specific functions for microsaccades. On a short time scale, microsaccades enhanced perception by increasing fixation errors. On a long time scale, microsaccades reduced fixation errors and binocular disparity (relative to pure drift movements). Thus, our findings clarify the role of oculomotor processes during fixation.*

Even when observers fixate a stationary object, their eyes perform extremely small movements. These fixational eye movements with small amplitudes are generated involuntarily, and observers are unaware of them (Ratliff & Riggs, 1950). It is widely assumed that they counteract retinal adaptation: If miniature eye movements are suppressed experimentally, retinal adaptation to the constant input induces perceptual fading within a few seconds (Ditchburn & Ginsborg, 1952; Riggs, Ratliff, Cornsweet, & Cornsweet, 1953). Therefore, identifying the specific functions of two important types of fixational eye movements, drift and microsaccades, has been an open research problem. Drift is a low-velocity movement with a peak velocity below 30 min arc per second. Microsaccades are rapid small-amplitude movements (Ditchburn, 1973), which typically occur at a rate of one to two per second, and have amplitudes that are rarely larger than 1° (Figs. 1a and 1b).

Cornsweet (1956) suspected that microsaccades serve to correct for a random drift of eyes. However, Nachmias (1959) showed that microsaccades were both error producing and error correcting, at different times (see also Kowler, 1991). Moreover, microsaccades can be suppressed voluntarily in high-acuity observation tasks such as laboratory analogues of threading a needle or shooting a rifle (Bridgeman & Palca, 1980; Findlay, 1974; Steinman, Cunitz, Timberlake, & Herman, 1967; Winterson & Collewijn, 1976). Consequently, it was concluded that microsaccades serve no useful purpose, and even that they represent an evolutionary puzzle (Kowler & Steinman, 1980; for a recent review, see Martinez-Conde, Macknik, & Hubel, 2004). Recently, their existence outside the laboratory was questioned (Malinov, Epelboim, Herst, & Steinman, 2000). Nevertheless, in this study, we reevaluated Cornsweet's (1956) hypothesis about the potential function of microsaccades with an approach originally developed for the analysis of human posture control (Collins & DeLuca, 1993, 1994).

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RANDOM-WALK ANALYSIS

A typical trajectory of the eyes during fixation is rather erratic and shows statistical features of a random walk (Figs. 1a and 1b). Our work was motivated by the observation that fixational eye movements are similar to center-of-pressure trajectories in human posture control (Balasubramaniam & Wing, 2002; Collins & DeLuca, 1993). In the analysis of random walks, the mean square displacement $\langle \Delta x^2 \rangle$ (relative to an arbitrary baseline) of a trajectory is studied as a function of the time interval Δt. To generalize classical Brownian motion (Einstein, 1905), Mandelbrot and van Ness (1968) introduced fractional Brownian motion to account for processes obeying a scaling law of the functional form

$$\langle \Delta x^2 \rangle \propto \Delta t^H \qquad (1)$$

where the scaling exponent[1] H can be any real number between 0 and 2. In classical Brownian motion, the sequence of displacements is uncorrelated, which leads to an exponent H equal to 1. When H is greater than 1, the random walk will have the tendency to continue to move in the current direction; that is, subsequent increments of the trajectory are positively correlated. This property is known as persistence. The opposite case, referred to as antipersistence, occurs for H less than 1. In this case, subsequent increments of the random walk are negatively correlated. Thus, fractional Brownian motion can serve as a mathematical reference for studying correlations in fixational eye movements across time. In this report, we show that a corresponding analysis helps to identify specific functions of microsaccades.

[1]Often the definition $\langle \Delta x^2 \rangle \propto \Delta t^{2H'}$ is used for the scaling exponent H', which leads to a range of $0 < H' < 1$—with H' equal to .5 for the special case of Brownian motion (Mandelbrot & van Ness, 1968).

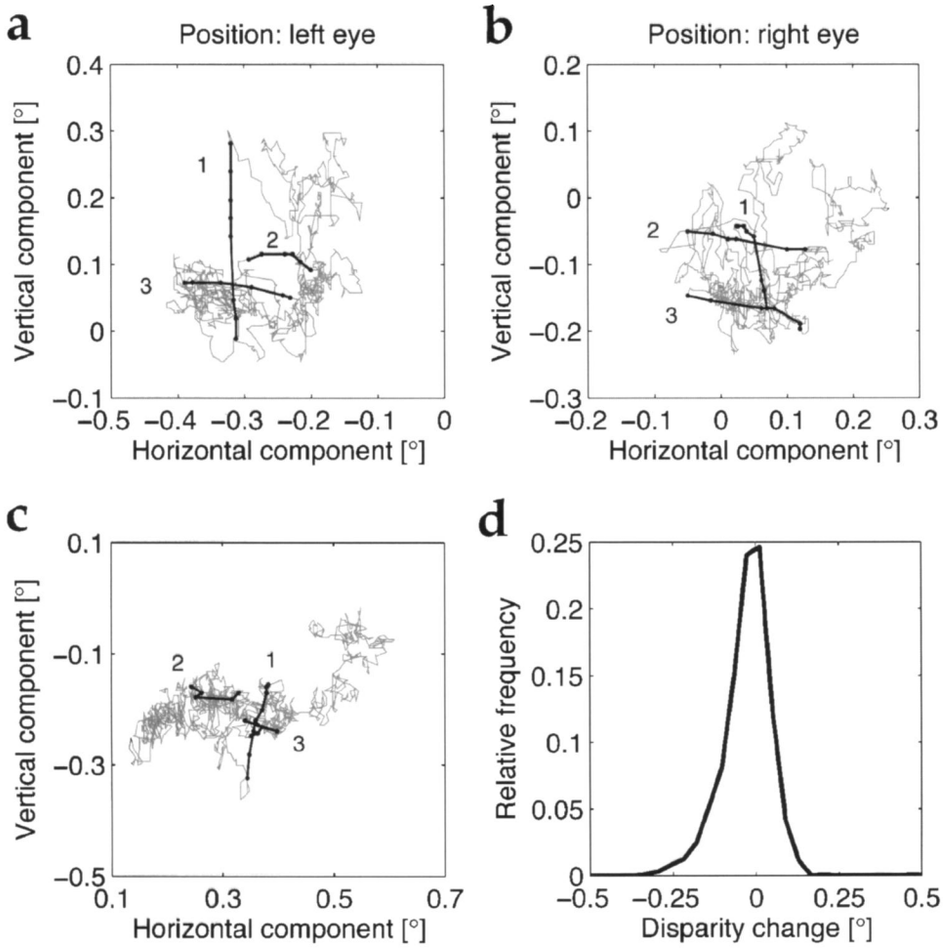

Fig. 1. Miniature eye movements during fixation: example trajectories (thin gray lines) of the left eye (a) and right eye (b) during a fixation of 3 s, (c) plot of the corresponding time series of the binocular disparity (the series of binocular differences of eye fixation positions), and (d) plot of the distribution of the difference in binocular disparity before and after each microsaccade (1,705 microsaccades observed in 490 trials from all participants). In (a), (b), and (c), microsaccades are shown with bold lines (marked by numbers); the microsaccades are more linear (ballistic) movement epochs embedded in the random walk.

METHOD

Participants

Five participants, the 2 authors and 3 students at the University of Potsdam, Germany, took part in the experiment.

Task

Participants were required to fixate a small stimulus (black square on a white background, 3 × 3 pixels on a computer display) with a spatial extent of 0.12°, or 7.2 arc min. Each participant performed 100 trials with a duration of 3 s.

Eye Movement Recording

Eye movements were recorded using an EyeLink-II system (SR Research, Osgoode, Ontario, Canada) with a sampling rate of 500 Hz and an instrument spatial resolution less than 0.005°. During preprocessing, 10 trials had to be discarded because of missing data samples.

Data Analysis

In the first step of our analysis, we computed the temporal evolution of the mean square displacement $\langle \Delta x^2 \rangle$ during fixational eye movements. To estimate $\langle \Delta x^2 \rangle$ (Equation 1), we introduced the displacement estimator $D^2(m)$, which is based on time-averaging over a single trajectory (Collins & DeLuca, 1993) represented by a two-dimensional (2D) time series $\{\vec{x}_i\}$,

$$D^2(m) = \frac{1}{N-m} \sum_{i=1}^{N-m} \|\vec{x}_{i+m} - \vec{x}_i\|^2 \qquad (2)$$

where N is the number of samples in the recorded time series and m is the time lag measured as the number of data samples; data were sampled every 2 ms, so the time lag is given by $\Delta t = m \cdot 2$ ms. According to Equation 1, the scaling exponent H can be obtained by

calculating the slope of a log-log plot of D^2 versus Δt. It is important to note that the value of D^2 cannot be biased by errors in absolute gaze position due to calibration errors of the eye tracker, because D^2 is a measure of the relative distance of data points within a trajectory (i.e., not distance to an intended fixation position).

Detection of Microsaccades

Microsaccades were detected in 2D velocity space using thresholds for peak velocity and minimum duration (Engbert & Kliegl, 2003b). We used a relative threshold of 6 *SD*s of the velocity and a minimal duration of 8 ms (or four data samples). Velocities $\{\vec{v}_i\}$ were computed from the series of eye positions $\{\vec{x}_i\}$ as $\vec{v}_i = T_0(\vec{x}_{i+1} - \vec{x}_{i-1})/2$, where T_0 was the sampling rate of 500 Hz. Furthermore, we considered only binocular microsaccades, that is, microsaccades detected in both eyes with temporal overlap (Engbert & Kliegl, 2003a). We also performed a control analysis using a 4-*SD* threshold to rule out a potential bias from undetected microsaccades. This variation of the detection threshold did not change the pattern of results.

RESULTS

Random-Walk Analysis

We started with an analysis of the combined effect of drift and microsaccades by applying the random-walk analysis to the recorded eye movement trajectories. A double-logarithmic plot of displacement D^2 as a function of time lag Δt uncovered two different time scales, indicated by two different slopes in Figures 2a and 2b. On the short time scale from 2 ms to 20 ms, we found persistent behavior ($H_S > 1$), whereas fixational eye movements were antipersistent ($H_L < 1$) on the long time scale between 100 ms and 400 ms. (The subscripts "S" and

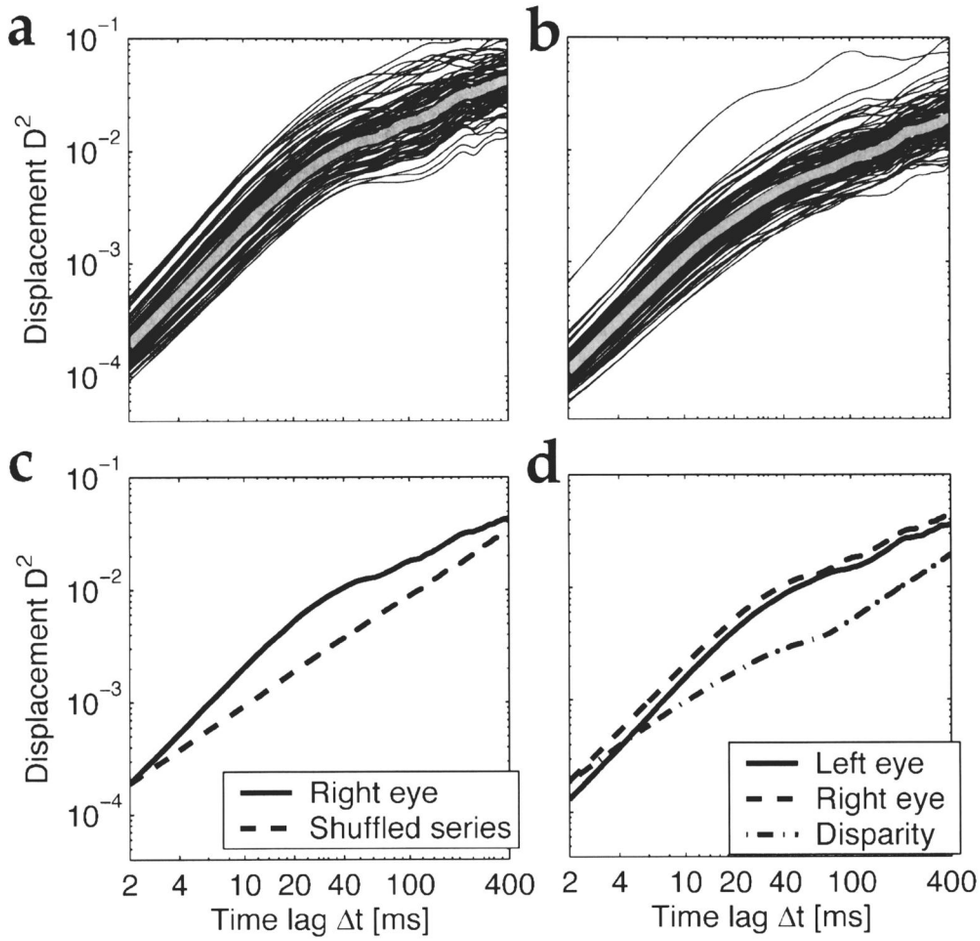

Fig. 2. Diffusion plots of the displacement D^2 versus time lag Δt. The plots in (a) and (b) show displacement of the right eye for all time series (black lines) for Participants 1 and 2, respectively; the gray line in each plot indicates the median over all trials. Two linear parts are evident in each plot, a short time scale (2 to 20 ms) and a long time scale (100 to 400 ms). Values of the scaling exponent for these two time scales for all 5 participants are presented in Table 1. The graph in (c) shows the median diffusion plots of the right eye for Participant 1 and for randomly shuffled surrogates. In randomly shuffled surrogates, all correlations are destroyed, which yields an exponent close to 1. The graph in (d) shows the median diffusion plots for the left eye, the right eye, and binocular disparity for Participant 1. On the short time scale, random walks of the left and right eyes are persistent, whereas the disparity is an uncorrelated random walk. On the long time scale, all three trajectories are antipersistent (see Table 1 for numerical values).

"L" refer to the slopes on the short and long time scales, respectively.) Thus, over short time intervals, there were positive correlations between subsequent increments of each eye's fixational random walk. This is psychologically plausible, because persistent behavior increases retinal image shifts, which contribute to the prevention of perceptual fading. However, if this persistent behavior were to continue over longer time intervals, the intended fixation point would be lost. Antipersistent fluctuations (i.e., negatively correlated increments of the random walk's trajectory) on the longer time scale serve to reduce the probability for such a disalignment.

To test this result statistically, we constructed artificial time series with randomly shuffled increments $\Delta\vec{x}_i = \vec{x}_i - \vec{x}_{i-1}$, that is, with surrogate data derived from the original time series of eye positions (Collins & DeLuca, 1993, 1994; Theiler, Eubank, Longtin, Galdrikian, & Farmer, 1992). This procedure removes all temporal correlations within the time series. The random-walk analysis of the scaling exponent on these surrogate data yielded a linear increase of D^2 as a function of Δt, that is, classical Brownian motion with H equal to 1 (Fig. 2c). The same analysis was applied to the time series of binocular disparities (Fig. 1c), which we defined as the differences (D) of fixations positions of the left (L) and right (R) eyes, $\vec{x}_i^{\,D} = \vec{x}_i^{\,L} - \vec{x}_i^{\,R}$. A comparison of the displacements D^2 for binocular disparity and single eye positions indicated that the slopes in the diffusion plots for the right and left eyes were very close to the slope for the series of binocular disparities (Fig. 2d).

Table 1 summarizes the results from the random-walk analysis of the experimental data and randomly shuffled time series for all 5 participants. In all cases, on the short time scale, the random walks were persistent in both eyes ($H_S^{R,L} > 1$) and uncorrelated between the eyes ($H_S^D \approx 1$). On the long time scale, all three scaling exponents indicated antipersistent behavior in the experimental data; however, the random-walk analysis suggested that the value for H_L^D was not significantly different from 1.

TABLE 1

Scaling Exponents From the Random-Walk Analyses

Participant	Short time scale			Long time scale		
	H_S^D	H_S^R	H_S^L	H_L^D	H_L^R	H_L^L
	Experimental data					
1	0.95	1.37	1.35	0.83	0.64	0.67
2	1.03	1.36	1.40	0.92	0.65	0.71
3	0.96	1.33	1.40	0.94	0.75	0.70
4	0.98	1.46	1.52	0.95	0.65	0.62
5	0.95	1.28	1.31	0.91	0.86	0.76
Mean	0.99	1.36	1.40	0.89	0.70	0.69
SD	0.10	0.11	0.11	0.23	0.26	0.25
	Randomly shuffled surrogates					
1	1.00	1.00	1.00	0.91	0.94	0.93
2	1.00	1.00	1.00	0.91	0.93	0.91
3	1.00	0.99	0.99	0.87	0.95	0.96
4	1.00	1.00	1.00	0.92	0.91	0.91
5	1.00	1.00	1.00	0.93	1.00	0.93
Mean	1.00	1.00	1.00	0.91	0.93	0.93
SD	0.03	0.04	0.04	0.19	0.19	0.20
	Microsaccades removed					
1	0.96	1.30	1.28	1.01	1.05	0.89
2	0.99	1.24	1.30	1.22	1.09	0.99
3	0.99	1.25	1.38	0.99	1.03	0.98
4	1.00	1.38	1.42	0.99	0.99	1.03
5	0.95	1.17	1.21	0.96	1.05	1.00
Mean	0.98	1.26	1.32	1.03	1.02	0.97
SD	0.05	0.10	0.10	0.21	0.22	0.21
	Random sequences removed					
1	0.95	1.37	1.34	0.83	0.66	0.66
2	1.03	1.36	1.40	0.91	0.69	0.72
3	0.96	1.32	1.40	0.94	0.73	0.70
4	0.98	1.46	1.51	0.95	0.66	0.64
5	0.94	1.27	1.31	0.90	0.89	0.76
Mean	0.99	1.36	1.39	0.89	0.72	0.70
SD	0.10	0.11	0.11	0.23	0.26	0.25

Note. The exponents were estimated by linear regression. Values for the short time scale, Δt = 2 to 20 ms, are indicated by subscript "S," and values for the long time scale, Δt = 100 to 400 ms, are indicated by subscript "L." Superscript "D" = disparity, and superscripts "R" and "L" = right and left eyes, respectively. Standard deviations were computed over all trials from all participants (N = 490).

The Function of Microsaccades

In the next step, we extended the random-walk analysis to explore the potential role of microsaccades. The microsaccade rate ranged from 0.8 to 1.9 s^{-1} across participants. The contribution of a microsaccade to the control of binocular disparity is given by the difference between disparity after the microsaccade and before the microsaccade. The mean contribution of all microsaccades to binocular disparity turned out to be error correcting, that is, negative ($M = -0.036°$); however, the distribution was rather broad ($SD = 0.094°$), so that 35% of all microsaccades were error producing (see Fig. 1d). This result is in good agreement with previous findings (Kowler, 1991; Nachmias, 1959).

To evaluate the function of microsaccades for binocular coordination, we computed the time series of increments (velocities), removed all data samples corresponding to microsaccades, and reconstructed the trajectories by computing the cumulative sum of increments. In this way, we removed on average 32.9 data samples (or 2.2%) from the series of 1,500 samples in each trajectory to obtain an artificial trajectory without microsaccades, which permitted the analysis of the contribution of microsaccades to the fixational random walk. Then, we compared the scaling exponent obtained for the original trajectory and the exponent estimated from the trajectory without microsaccades to isolate the effect of microsaccades (Table 1).

On the short time scale, microsaccades enhanced the persistence of the random walks of the right and left eyes; the scaling exponents for the right eye decreased from an average value of 1.36 in the experimental data to 1.26 for the sequences with microsaccades removed, and numerical values for the left eye were comparable. The scaling exponent for the disparity remained at a value very close to 1; that is, both microsaccades and drift were uncorrelated on the short time scale. On the long time scale, however, the scaling exponents for both the trajectories of the eyes and the disparity increased for the sequences with microsaccades removed. For the disparity, the average value of the scaling exponent increased from 0.89 to 1.03. Thus, microsaccades were responsible for the antipersistent behavior on the long time scale. The data in Table 1 indicate that microsaccades also contributed to antipersistence of left and right eye movements. This

analysis suggests that drift by itself is also antipersistent on the long time scale.

To check this pattern of results computationally, we again constructed surrogate trajectories, removing randomly chosen parts of the trajectories (with the same lengths as the microsaccade sequences). The scaling exponents obtained with this procedure did not differ from those obtained with the original time series. Thus, the effect we obtained was indeed due to microsaccades.

DISCUSSION

Microsaccades play a key role in correcting fixation position and controlling binocular disparity. This proposition was supported by a random-walk analysis in which we discovered two different time scales in the statistics of fixational eye movements. This time-scale separation helps to resolve previously contradicting experimental results reported for microsaccades, namely, that they are both error producing and error correcting (Kowler & Steinman, 1980; Nachmias, 1959). On a short time scale up to 20 ms, microsaccades help to counteract retinal adaptation (Ditchburn & Ginsborg, 1952; Riggs et al., 1953) by increasing the persistence of the eyes' random walk. On the long time scale, however, microsaccades are error reducing (relative to an uncorrelated random walk) for fixation positions of the eyes, as well as for binocular disparity.

This study of micromovements of the eyes is a further example of a useful interdisciplinary application of methods from statistical physics to behavioral processes (Balasubramaniam & Wing, 2002; Collins & DeLuca, 1993, 1994). Recently, theoretical models for transitions from persistent to antipersistent correlations in biological systems have been proposed (Liebovitch & Yang, 1997). These models suggest that a system's inertia might produce persistence, whereas a limited system size can be a source of antipersistent correlations. Applying such theoretical models to the problem of fixational eye movements seems a promising approach for understanding the dynamic behavior of the human oculomotor system in greater detail.

The function of microsaccades has been puzzling because microsaccades can be suppressed voluntarily (Bridgeman & Palca, 1980; Winterson & Collewijn, 1976). Recently, we found that simple display changes (e.g., a change in the color of a fixation cross) can also reduce the microsaccade rate. In our study, however, some hundred milliseconds later an increase in microsaccade rate beyond the base rate compensated for the earlier suppression. Thus, in earlier studies, microsaccades might have been only delayed rather than suppressed (Engbert & Kliegl, 2003b). Therefore, the fact that one can suppress microsaccades does not provide strong evidence against their functional relevance. Moreover, in a previous study (Engbert & Kliegl, 2003b), we found that microsaccade orientation also indicated reliably the direction of *covert* attention shifts in Posner cuing paradigms.

Our results are compatible with recent neurophysiological findings about effects of microsaccades on visual information processing (Leopold & Logothetis, 1998; Martinez-Conde, Macknik, & Hubel, 2000, 2002). For example, recently microsaccades were shown to generate bursts of spikes in primary visual cortex (Martinez-Conde et al., 2000); this promising finding might help clarify the way in which microsaccades enhance perception during free viewing of a stationary scene. Taken together, these neurophysiological findings and the results reported here suggest that microsaccades serve a useful purpose on both the oculomotor (behavioral) and the neurophysiological levels after all.

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